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This project was successful in examining the neural mechanisms involved in attention. An important outcome is the conclusion that modification of neural transmission by attentional processes takes place in many different places in the nervous system, and at many different levels of information processing. Animal models of attentional processes are being developed that allow more extensive analysis of the neuroplastic changes involved in attention. The field of attention is now able to proceed in an integrated fashion similar to the way that memory has been pursued.

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Table of Contents

Attention and Cognitive Neuroscience	3
Experimental Strategies to Investigate the Neuronal	
Correlates of Selective Attention	10
The Locus of Spatial Attention	17
Plasticity of Cortical Receptive Fields	26
Pulvinar and Orienting of Attention	28
Parietal Lobe and Shifting of Visual Spatial Attention	32
Selective and Divided Attention	35
Dysfunction of Attention	39
The Element Superiority Effect: Attention?	46
Animal Models of Attention Deficit	47
Conditioned Attention Theory	50

ATTENTION AND COGNITIVE NEUROSCIENCE

The entire behavioral repertoire of any individual is immense. We can respond to many different stimuli in many different ways. Yet, we actually do respond to only a few stimuli in a few ways. Thus, out of the full spectrum of our possible behaviors, some behaviors are selectively enhanced relative to others. Attention is one of the cognitive processes that allows us to determine which of the stimuli are selected.

What is attention? Throughout the years, a number of definitions have been used to describe the attentional process. A common feature of these definitions is that attention is a selective process. The selection of certain information at the expense of other information decreases the amount of information that must be processed by the brain. Thus, attention is the differential processing of simultaneous sources of information as consequence of task demand.

Some of the immediate questions that come to mind concerning the neural mechanisms of attention are: what, when, where, how, why. The first set of questions concerns the site of the transformation of input to output.

What is this transformation?

Where is it located?

How does modification take place?

When does modification take place?

Why does modification take place?

The second set of these questions has to do with the system

that does the modulation.

What is the modulation mechanism?

Where is the modulation mechanism located?

How does modulation take place?

When does modulation take place?

Why does modulation take place?

Given that an individual is capable of at least two different responses, what are the variables that influence the relative probability of one response as compared to another? Several alternatives are possible. All of them have in common an enhancement of one system relative to another. However, many of the mechanistic questions cannot be addressed with behavioral analyses, but must be addressed with neural ones because only neural ones allow direct access to the components of the system, where these questions must be answered.

The fact that we typically use the term "attention" in the singular rather than the plural, suggests that a cognitive model might have only a single module for attention. The considerable discussion of attention as either "early" or "late" was initially phrased in such a way to assume that attention took place only once, either early or late. Even an intermediate approach that considers the possibility of both early and late selection is much too limited, however. The modulation of sensory information produced by attention must occur many times. Indeed, rather than being singular, unique, and restricted, attention must be plural, common, and ubiquitous. Thus, the goal of this enterprise should not be conceptualized as an attempt to find the neural mechanism of

a single attentional process. Rather, the goal must be more ecumenical, and consider the possibility that many cognitive and neural mechanisms should be discussed in terms of attentional processes.

An extreme view could propose that attentional processes can occur at every synapse in the central nervous system, providing a mind boggling list of alternatives (approximately 10 billion neurons each with one thousand synapses, approximately 10^{14} synapses). Even if this estimate is wrong by several orders of magnitude, an understanding of attentional mechanisms must inevitably take a pluralistic rather than a unitarian approach. First, the topics covered here indicate a multiplicity of neural structures participating in attentional processes. Second, the synaptic organization of the nervous system provides even more opportunities, and we have no reason to believe that our current knowledge is complete.

Modulation of an input-output system can take place for many reasons. Psychological variables include learning, motivation, and arousal. How is attention distinguished from these other mechanisms? An obviously tempting answer is to say that attention is what is studied in experiments conducted by people who study attention. Although such an answer has immediate intuitive appeal because it solves a difficult problem now, it obviously has no enduring appeal because anyone can then define the field of attention simply by saying that they are studying it. Some principled basis is necessary to decide whether a phenomenon of modulation is to be categorized as involving attention or some

other psychological process. That issue will not be easily resolved here. Indeed, the nagging possibility is always present that the mechanisms of modulation may be the same in all circumstances, and the name that we put on the mechanisms of modulation reflects arbitrary categorization for the convenience of the experimenter rather than fundamental distinctions that are present in the world. In any case, we have determined four different characteristics of attention, which we hope can serve as a guideline.

1. Attention produces a shift in sensitivity or discriminability. Thus, attention produces an increase in the ability to discriminate a signal from associated noise.
2. Attention is associated with costs and benefits. The benefit for selected stimuli is faster detection and responding. The cost for nonselected stimuli is worse detection and slower responding.
3. Attention is independent of shifts in criterion. That is, attention is not directly correlated with changes in response bias.
4. Attention is generally changed rapidly.

Divided attention is not necessarily a different process than selective attention, but is a case where selection is occurring simultaneously for two or more elements in the environment. Thus, divided attention can be thought of as sharing the processes of selective attention that are involved in the selection process. In addition, a second component may monitor and divide the selection

process so that more than one item can receive attention. This second component may be one that allows for sharing of attentional capacity, or it may time share the selection process so that selection switches back and forth or switches between the items that are attended.

Integration of Psychology and Neuroscience

One of the first things that must be accomplished in any endeavor to link different fields of study is to specify the level of analysis. Each field may describe results in a particular level focus of organization. The methodology used by a particular field may bias the viewpoint of certain levels. A complete description of attention requires many different levels of organization. Three general categories of languages are used. These are: operational, psychological, neural.

Operational descriptions are empirical and describe the actual manipulations and measurements of independent and dependent variables, respectively, as conducted in an experiment. This language is the one of experimental procedures, describing the ways in which an experiment proceeds. Some examples include: presentation of a stimulus, measurement of a response, calculation of reaction time, placement of a lesion in the brain, recording of electrophysiological activity.

Psychological or cognitive descriptions use terms that make inferences about the organization of processes that accompany the behavior. Terms include ones such as: attention, early selection,

response selection, filter decision stage. This language is designed to provide a description of the ways in which psychological processes can describe the phenomena observed in the experiment.

Neural descriptions use anatomical, electrophysiological or neurochemical terminology to describe the mechanisms involved in the operational descriptions. In the same way that psychological explanations provide a cognitive description of the mechanisms involved in behavior, so the neural language provides a description in terms of the brain.

Cognitive neuroscience seeks to identify the relations between cognitive processes and neural ones. In essence, this goal can be considered similar to that in translating one language to another. In this analogy, mental and neural descriptions are two different languages describing the same phenomenon. The translation process occurs by first describing each of the languages individually, and then indicating the ways in which the two are related.

In reality, of course, this translation process deals not with just a single pair of languages, but with many different ones. The brain has many neural descriptions: anatomical, electrophysiological, neurochemical, etc. Likewise, the mind has numerous descriptions too: cognitive, computational, etc. For the moment, however, we are going to consider the limited domain of a single neural language and a single cognitive one. The principles outlined here hold for any pair of cognitive and neural languages.

At every level of inspection, the brain is heterogeneous. Even the casual visual inspection of a whole brain shows that it is

composed of various bumps, grooves, and varies in consistency, from relatively tough to very amorphous. At every more molecular level of description, this same heterogeneity persists. In one nucleus of the brain, nerve cells are different than those in another nucleus. For a given nerve cell, the different parts of the cell (axon, dendrites) look different. Within the membrane of a nerve cell, the protein structure varies from one location to another.

Some have argued that useful information about the structure of cognitive processes can be gathered from the study of brain damaged individuals without regard to the location of that damage, and without regard to an understanding of the functional organization of the brain. In essence, the basic argument is as follows. If a lesion produces a dissociation so that one cognitive process is disrupted while another is intact, then those two cognitive processes must be independent modules in the cognitive analyses. In some very limited sense, this argument has some validity. However, it has two severe logical limitations.

The first is within the experimental design itself. Many dissociations are ultimately uninterpretable for two reasons. First, the experimental design fails to obtain the necessary quantitative information about the effects of parametric manipulations on the dissociation, or the parametric results that are obtained do not allow unambiguous conclusions about the independence of cognitive processes. These points have been discussed in many different reviews, and will not be discussed again here. The major point is that substantial parametric analyses with converging operations are critical to make accurate

inferences about the organization of cognitive structure.

The second issue concerns the limitations that result from a failure to consider the brain as a system. The function of a given area is its transformation of its input to its output. Consequently, a functional analysis can proceed only with a systematic view of the area in question, considering both its afferents and its efferents.

Finally, consider the peculiar state of affairs that would result if neuroscientists took this same view, and argued that an understanding of psychology was unnecessary for the cognitive neuroscience endeavor as described here. If simultaneously psychologists ignore the brain and neuroscientists ignore the mind, no effective translation between the two is likely to take place. For all these reasons, any effective integration of mind and brain must give full recognition to both endeavors.

EXPERIMENTAL STRATEGIES TO INVESTIGATE THE NEURONAL CORRELATES OF SELECTIVE ATTENTION

One powerful technique to relate neural and cognitive explanations of behavior is single unit recording during behavioral tasks. Because the animal is behaving, all of the standard psychological manipulations and measurements can be made. Because single unit activity is being recorded, the responses of these fundamental neural components can be related to specific psychological processes. This approach has been spectacularly successful in analyzing sensory systems, and the same strategies

can be used to examine cognitive, attentional ones as well.

The challenge, as in many experiments, is proceeding from theoretical statements to empirical data and back again. Obtaining empirical data about correlations between single unit activity and behavior is relatively easy given all of the technical advances in psychology and biomedical engineering. However, interpreting the empirical data in terms of attentional mechanisms requires careful experimental design and analysis of the obtained data. Many experiments have used variations of a basic theme, which is outlined here.

A fundamental question that is often asked concerns the extent to which attention alters the processing of sensory stimuli. If selective attention is active, then reactions to some stimuli should be enhanced relative to reactions to other stimuli. If the modulatory mechanism of selective attention takes place prior to the neurons from which activity is being recorded, then the activity of those neurons should change as a function of selective attention. Assuming that "bigger is better" for most neural signals, the neural response to a given stimulus should be greater when selective attention is directed to that stimulus than when selective attention is not directed to it. The challenge comes in being certain that any change in neural activity in response to a change in selective attention is due to the attentional mechanisms, rather than some other mechanisms.

One major step in this direction is maintaining the same physical stimulation while varying the demand of selective attention. Neuronal activity can easily be influenced by the

presentation of the different stimuli. Consequently, any experimental procedure that simultaneously alters the attentional demand and the configuration of stimuli presented to the animal risks confounding an attentional explanation with a sensory one.

This strategy has many different variations. In all of them, the instructions to the animal are provided by one or more trials prior to the trial of interest. For example, on the trials of interest, a compound stimulus may be presented to the animal. Prior to these trials, reinforcement is given for responding on the basis of one or more of the elements in this compound stimulus.

One example of this procedure is that used to examine the effects of attention on the responses of single units in several components of the visual system: pulvinar, parietal cortex, and frontal cortex. Each trial begins with the monkey fixating on a small dot of light in the middle of the visual field. A stimulus is then presented in the periphery. Selective attention is directed to either the fixation point or to the peripheral stimulus by training with selective reinforcement. Selective attention is manipulated by varying the stimulus that dims and signals the time to make a response to obtain reinforcement. To focus attention on the fixation point, a series of trials is given in which the fixation point dims at some time after the onset of the peripheral stimulus. To focus attention on the peripheral stimulus, the monkey is given a series of trials in which the peripheral stimulus dims. Responses produce reinforcement only when they are made soon after the stimulus dims. Because the stimuli are near the threshold of perception, the monkey must focus his eyes on them and

attend to them in order to respond at the appropriate time and obtain reinforcement. Consequently, the training prior to the trials on which single unit activity is recorded provides the instructions to direct attention to either the fixation point or the peripheral stimulus. Performance during the trials on which activity is recorded provides a check to be certain that attention is still directed to the appropriate stimulus.

All approaches examining the effects of expectancy on performance use a similar experimental strategy. Examples include: search image of predators seeking prey, latent inhibition, and simple expectancy effects. In all of these, the stimuli presented for the critical tests are identical. Attention is manipulated by experience prior to the test, with trials that provide differential reinforcement for responding to some stimuli as compared to others.

A second component of the experimental strategy is to control for changes in arousal and in responses. The demand for selective attention may in itself be sufficient to alter both neural and cognitive processes. Consequently, the experiments that manipulate selective attention often seek to alter the direction of that selective attention. If the demand for selective attention itself is the critical variable, then neural activity should change when selective attention is required regardless of the stimulus to which that selection is directed. Alternatively, if the selection process itself is important, then neural activity should change when attention is directed towards some stimuli rather than others. If the changes in neural activity reflect the increased demands due to arousal, then the direction of attention should not have an

effect on these neurons. If the increased neural activity reflects the direction of attention to a particular stimulus, then neural activity should increase only when that stimulus is presented but not when another stimulus is presented.

A second issue concerns the possible influence of response mechanisms on the neural activity. In order to demonstrate selective attention to a given stimulus, some response is necessary. The type of response may influence neural activity. Consequently, a second manipulation concerns the extent to which a change in neural activity is related to one particular response system.

A variation of the procedures used for monkeys described above can again be used to illustrate these issues of response control. In both types of trials, the stimulus presentation is as described above. A small light is presented at the fixation point. The monkey fixates that spot. A peripheral stimulus is turned on. When that stimulus dims, the monkey makes a response. In one case, a saccade is made to the peripheral stimulus, which then dims, and the response is to lift the lever. In a second case, the eye remains focused on the fixation point, the peripheral stimulus dims, and the monkey responds by reaching with his paw to make a response. As usual, neural recording is made at the onset of the peripheral stimulus, before any of these responses take place. In the frontal eye fields, enhancement of neural activity, relative to the baseline, takes place only in the saccade task, indicating that neural activity is altered only when the response is an eye movement, suggesting that the neural enhancement is related to a

particular motor system. In the parietal cortex, the neural enhancement occurs in both tasks, indicating that the response requirement is not influential. This pattern of results suggests that the enhancement in the parietal cortex reflects a generalized increase in neural responsiveness to the stimulus at a relatively peripheral aspect of the system, allowing for coordination with many different response systems. In contrast, the activity in the frontal eye fields appears to be more towards the output side of the system, related to a particular response system. In the system of neural enhancement examined here, the parietal cortex ought to be more towards the input as compared to the frontal eye fields. An examination of response latency could help to test this hypothesis. These results are also relevant to cognitive analyses and indicate that selection takes place at many points during cognitive processing, not just "early" or "late."

Information Processing

A simple model of information processing can be constructed from four stages. (1) Encode: the process of perceiving the stimulus. (2) Identify: identification by scanning a list in memory. (3) Decide: choosing the appropriate response to the stimulus is determined. (4) Respond: making the response. Both sensitivity and criterion shifts can change responding. Changes in sensitivity should be due to alterations in stages prior to the decide stage. Criterion shifts should be due to changes in stages that follow the decide stage. Given that attention is associated

with changes in sensitivity, attentional processes should act on either the encode stage, the identify stage, or both. Most researchers agree that attentional processes affect perceptual stages of information transmission. A more controversial, but broader, view of attention would include alterations of motor and many other stages.

Locus of selection

The locus of selection as it relates to attention has been debated for a number of years by cognitive psychologists. This is the classic debate of early selection versus late selection. Broadbent was one of the first to propose that attention filtered out information at an early stage in information processing. This theory suggested that information is filtered before the identification stage. Late selection theories as proposed by Deuch & Deuch and Norman suggest that information is processed and identified and that unattended information is filtered out after the identification stage. Early and late selection are two extreme views of the locus of selection. Other investigators have proposed a mixed selection such that the locus occurs neither at an early stage nor at a late stage. The basic question is the identification of the locus of selection of information travelling from the sensory input to the motor output. Other questions associated with the location of the selection process are the following: Is the process hardwired or is it modifiable? If the location is modifiable, what determines this modification? For

example, can task difficulty influence the location of selection? Does the location of the selection process depend on the sensory modality of the stimulus that is being attended? How is selection accomplished? In other words, what are the mechanisms by which certain stimuli are selected? What is the fate of unattended stimuli? What controls the selection process? What happens to the attended stimulus when attention is manipulated? These are all questions for which studies on the neurobiology of attention have at least partial answers.

THE LOCUS OF SPATIAL ATTENTION

The ability to attend to independent events in different locations in space is influenced by the spatial proximity of those events. If the events are very close together, attending to one may interfere with attending to another. If, however, they are relatively far apart, attending to one may be able to proceed without detriment in attending to the other.

Neuronal activity in two cortical areas, visual area 4 (V4) and inferotemporal cortex (IT) was altered by changes in spatial attention. In both areas, the size of the receptive field and the firing rate of a stimulus located within the receptive field were altered by attention. Within the receptive field, changes in the locus of attention influenced the response of the neurons. Outside of this receptive field (a result that could be obtained only for the V4 neurons because of technical reasons), the locus of attention had no effect on responsiveness. This pattern of results

suggests that these visual cortical areas must have multiple independent modules for visual attention. Within a given path, attention to the locus of one stimulus interferes with attention to the locus of a second stimulus. Between modules, no such interference takes place. If this principle is correct, the electrophysiological and neuroanatomical characteristics of the visual system will have a substantial effect on the extent to which attention to one locus will interfere with attention to another locus.

The experimental design used the strategy of presenting the same stimulus display in the critical conditions and manipulating attention by response-reinforcement contingencies. The behavioral task was a delayed conditional discrimination. For each trial, two locations were used to present a sample stimulus and a test stimulus. The two sample stimuli were presented simultaneously, the two test stimuli were presented simultaneously. Response-reinforcement contingencies directed the monkey's attention to one pair of sample-test stimuli rather than the other. The attended stimuli were the sample-test pair that determined the correctness of the response. The unattended stimuli were the sample-test pair that were irrelevant for the correct response.

For cells in both the V4 and IT cortex, the stimuli were bars of light that varied in color, size and orientation. Preliminary exploration of the neuron's receptive field identified two combinations of these characteristics. One combination, the effective stimulus, increased the rate of activity of the neuron when the stimulus was presented in the neuron's receptive field.

The other combination, the ineffective stimulus, did not alter the neuron's rate of response when presented in the same visual field.

When the monkey attended to the effective stimulus, the response rate of the neuron was greater than when the monkey attended to the ineffective stimulus, even though the physical stimulus display was the same in both cases. The magnitude of this effect was greater for cells in V4 than for cells in IT cortex, but was characteristic of the majority of neurons in both areas.

Within each stimulus display, the ineffective stimuli were by definition different than the effective stimuli because the two combinations of stimuli differed, by definition, in their ability to elicit responding in the neuron. Consequently, the attenuation produced by directing attention to the ineffective stimuli could have been produced by attention to the locus in which those stimuli were presented, or by attention to the physical characteristics of those stimuli (color, size, orientation). To distinguish between these two alternatives, the experimental procedures were changed so that the ineffective stimuli and the effective stimuli were randomly presented in each of the two locations. For the neurons tested with this procedure, the attenuation index did not change, indicating that the locus of attention, rather than the physical characteristics of the stimuli attended, produced the attenuation.

Neurons in both V4 and IT had this attenuation effect. However, the responses of these neurons differed into two other characteristics. (1) The magnitude of attenuation was greater in V4 neurons than IT neurons. (2) The size of the receptive field was greater in IT neurons (up to the limit of testing, which was 12

degrees in both the contralateral and ipsilateral visual fields) than for the V4 neurons, which had receptive fields 2-4 degrees in size. Whether these two characteristics are causally related remains to be determined. However, the combination of a smaller receptive field and a greater attenuation index in the V4 neurons obviously leads to a greater specificity in the processing of visual information.

Attention outside of the receptive field of a V4 neuron did not attenuate the neuron's response to the stimulus display. The experimental procedure was the same as described above except that the ineffective pair (sample and test stimuli) was located outside of the receptive field of the neuron. Attention to the ineffective stimuli did not alter the response of the neuron to the effective stimuli.

Consequently, V4 must have multiple independent modules for responding to visual stimuli. Within a module, defined electrophysiologically as the size of the neuron's receptive field, attention produces two complementary effects: enhancement of the neuron's responses to the attended stimuli, and decrement in the neuron's responses to the unattended stimuli. Between modules, electrophysiologically defined by boundaries between receptive fields, attention to one set of stimuli does not alter the responsiveness to another set of stimuli. If this pattern of results is true for every V4 neuron, and these neurons have small overlapping receptive fields, then many visual stimuli should be able to be processed simultaneously by the V4 neurons.

A similar analysis for IT neurons was not possible for

technical reasons. Because the receptive fields of these neurons included the entire test area, no stimuli could be presented outside of the receptive field. Determining whether such an effect does exist would be useful to provide a comprehensive comparison of V4 and IT neurons. However, the functional importance of such an effect for IT neurons must be minimal because of the large size of the receptive field.

V1 neurons also had no attenuation of responsiveness when attention was directed outside of their receptive field. However, this result is difficult to interpret. The receptive field of a V1 neuron was so small (less than one degree) that the monkey was unable to perform the test correctly when both stimuli were presented inside this receptive field. The absence of an effect of attention directed outside the receptive field might indicate a dissociation like that observed in V4 neurons, or it might reflect the absence of any kind of attentional effect on the responsiveness of V1 neurons. Distinguishing between these two alternative interpretations can be achieved only after the appropriate data are collected from an experiment presenting both sets of stimuli within the neuron's receptive field.

In summary, for both V4 and IT neurons, directing attention to one location or another within the receptive field of the neuron can have a substantial effect on the neuron's responsiveness to a stimulus. Within a receptive field, attention to the locus in which effective stimuli are presented enhances the responsiveness of the neuron relative to a condition directing attention to some other locus. For V4 neurons, the trade-off in responsiveness is

limited to the size of the neuron's receptive field because similar effects do not occur when attention is directed to ineffective stimuli at a locus outside of the receptive field. Consequently, within a small area, defined by the neuron's receptive field, direction of attention to onset of stimuli enhances processing of those stimuli at a cost to other stimuli, while in a larger area, this cost is not incurred. The data from this study provide evidence that the locus of spatial attention starts at area V4. Visual processing areas prior to V4, such as V1, were not altered by manipulations of attention.

The results of other work demonstrate that a second visual pathway is also altered by attention. A systematic series of experiments recording from single neurons in many different areas of the brain demonstrated a series of dissociations indicating that visual attention with or without saccadic eye movements can alter the rate of neuronal activity in response to the onset of a visual stimulus. In some brain areas, especially the frontal eye fields, a combination of attention to a stimulus and a saccadic eye movement produces the enhancement, whereas either attention or saccadic eye movements is insufficient. In other brain areas, such as the parietal cortex, only attention is necessary to produce the enhancement. This pattern of results provides information about the different ways in which attention and the intended response can influence the processing of spatial information, and this whole series of experiments is an excellent example of the way in which a systematic analysis can provide information about the neuronal mechanisms of attention.

Some discussions of these results make the assumption that the term "attention" can be applied only to an enhancement process that is independent of the response. Although such a definition can be defended, it is not required. Certainly, the generality of the enhancement effect is an important characteristic, and enhancement in several response systems suggests a process that may be more towards the perceptual side of the neural/mental processing system, whereas enhancement limited to a single response suggests that it may be more closely related to an output module. However, both types of enhancement can have a significant influence on the ability of the individual to respond to a stimulus, and certain circumstances can lead to a preferential advantage of each kind of enhancement.

The series of studies that have just been presented provide evidence that the locus of attention occurs relatively late in the visual system, in area V4, parietal cortex and frontal eye fields. In other sensory modalities, attention may have its effects at earlier stages of processing.

Locus of Attention in the Nonvisual systems

In a study of somatosensory attention, changes in neuronal activity associated with attention occurred in the medullary dorsal horn. Two experiments were performed. In the first, the effect of a relevant thermal stimulus (requiring a response) was compared to an irrelevant, unexpected thermal stimulus (not requiring a response). Neuronal activity in the medullary dorsal horn was

greater for the relevant stimulus compared to the irrelevant stimulus. In the second study, the same thermal stimulus was presented alone (relevant) or in conjunction with a visual task, in which case the thermal stimulus was irrelevant because the monkey responded to the visual stimulus. As in the first study, firing rate of medullary dorsal horn neurons was greater when the thermal stimulus was attended as compared to when the thermal stimulus was unattended.

In this study, neuronal activity was increased by an increase of attention to thermal stimuli. This modulation in the medullary dorsal horn occurred at a comparatively earlier stage in the system than in the visual system.

As in the somatosensory system, attention can have effects very early in the auditory system. Evoked oto-acoustic emissions (EOAE), a measure of activity of outer hair cells in the cochlea, were recorded during auditory clicks presented alone or in conjunction with a visual task. Active attention to a visual task attenuated the EOAEs. Thus, attention can modulate auditory signal very early in the auditory system.

The results of these studies illustrate the various locations that attention can modulate information processing. Attention is probably modulating visual information at sites in addition to area V4 and IT. Taken together, these illustrative examples suggest that attention can modulate neuronal processing. The modulation can occur both at early, as well as late, stages in information processing.

Does task difficulty alter attentional selection?

One possibility is that the locus of selection in the nervous system depends on the difficulty of the task. Easy tasks may have selection occurring early in the system, whereas difficult tasks may require more processing prior to selection. The influence of task difficulty on neuronal responses is described in the next chapter.

Numerous expressions in our everyday language imply that we vary the amount of attention that is given to a task: When the going gets tough, the tough get going. We often prepare ourselves to give just as much effort as is necessary to achieve the desired level of performance. Consequently, if the expected task is easy, we often "coast," preparing ourselves to commit only a minimal amount of psychological effort because that should be sufficient to perform adequately. If, however, the expected task is going to be very difficult, then we may summon more of our abilities to dedicate to the task because successful performance requires more effort.

One experimental design to address these questions is composed of easy trials and difficult trials, operationally defined in terms of their level of choice accuracy. The easy task is composed mainly of easy trials, and the difficult task is composed mainly of difficult trials. A blocked design can be used so that the instructions at the beginning of the test indicate the kinds of trials that are likely to occur.

If the nervous system also responds to differential attentional demands, presumably giving only what is necessary to attain the desired level of performance, then changes in task difficulty should alter neuronal activity. The results of this experiment demonstrate that many of the characteristics of neuronal activity in visual area 4 (V4) of the monkey change as a function of task difficulty, with the change being in the expected direction: the more difficult the task, the greater the selectivity and the greater the magnitude of the response of these neurons.

Some other unanswered questions include the following: the site of the mechanism that produced the neural modulation, the effects of this neural modulation on neural activity in areas of the brain that subsequently receive these signals, the possibility of other, independent sites of enhancement. All of these issues can be addressed empirically, and will place these observations in a more systematic framework. Even without this additional information, however, the fundamental point of the research is clear. An increased psychological demand for attention can produce increased sensitivity of the nervous system.

PLASTICITY OF CORTICAL RECEPTIVE FIELDS

At least some of the neural mechanisms leading to changes in receptive field properties in cortical neurons following attentional shifts may be similar to those examined in the receptive fields of the somatosensory system following pharmacological manipulations. In general, the GABAergic and

cholinergic systems provide important influences on the receptive field properties of neurons in the somatosensory cortex.

An anesthetized cat had multibarrel pipettes inserted into the somatosensory cortex (area 3B). Cholinergic and GABAergic drugs or glutamate were administered in the dendritic region of the cortical neuron. Mechanical stimulation mapped the receptive field of the neuron. In some studies, electrical stimulation of the basal forebrain region was used to release endogenous ACH into the cortex.

The involvement of the GABA system in regulation of the somatosensory receptive field was demonstrated using the GABAergic antagonist bicuculline. Bicuculline modulated the receptive fields in four ways. (1) The magnitude of the response to stimulation in the receptive field was increased. (2) The latency of the response was decreased. (3) The area of the receptive field was increased. (4) Some cells that were not previously activated by stimulation in the receptive field developed a response.

The cholinergic system can also influence the properties of the receptive field. ACH increased the magnitude of responses to cutaneous stimulation, sometimes activating previously silent neurons. The size of the receptive fields during ACH administration was not altered substantially. ACH can also sharpen receptive fields of neurons in the visual cortex and increase the signal to noise ratio of neurons in the somatosensory cortex.

These data provide evidence that a number of different transmitter systems may contribute to the modulation of receptive field properties during attention. Each transmitter system may

have slightly differing actions on the receptive field as demonstrated for the GABAergic and cholinergic systems. Given that attention is probably not a unitary process, each transmitter system may be activated during only specific types of attention and during specific phases of the attentional process.

PULVINAR AND ORIENTING OF ATTENTION

Two lines of evidence suggest that the pulvinar is importantly involved in visual spatial attention, certainly the engage function, and possibly also the disengage-shift function. (1) Visual attention, with saccadic eye movements and without these eye movements, enhances the discharge of single units in the dorsomedial part of the lateral pulvinar. (2) Temporary functional blockade of cells in this same area of the lateral pulvinar alters performance in experiments designed to measure the visual field expectancy effect. Both sets of experiments are conducted using variations of the visual attention tasks in primates.

Reversible inhibition of the activity of neurons in the Pdm altered reaction time in the visual field expectancy procedure in a manner to suggest that cells in the Pdm are involved in engaging attention and possibly shifting it. The reversible inhibition was produced by an intracranial infusion of muscimol, a GABA agonist, into the Pdm. The infusions were 1-5 micrograms in 1.0-1.5 microlitres.

The effect of muscimol was unilateral. In the ipsilateral valid cue (normal-normal) condition, muscimol had no effect on RT.

Consequently, all of the attentional processes in this conditions in the normal side of the brain were unaffected by the infusion of muscimol in the contralateral side.

Inhibition of Pdm cells had a substantial effect on the attentional processes involved in contralateral valid cue (drug-drug) trials. Muscimol increased mean RT at all three cue-target intervals, with the magnitude of the increase ranging from about 30 msec to about 50 msec. This increase in mean RT indicates that muscimol disrupted one or more of the psychological processes in the contralateral valid cue (drug-drug) trials: disengage the fixation point, move to the cue, engage the cue, engage the target, respond.

In another study, the magnitude of response of units in the Pdm to the onset of the stimulus display was enhanced when the monkey was instructed to saccade to or attend to the stimulus in the visual field, but not when the monkey was instructed to attend to the stimulus outside of the visual field. (1) Prior to the onset of the visual display, the unit had a low baseline of responding. (2) In the fixation task, which instructed the monkey to continue fixating the fixation point, the onset of the display increased the rate of firing, which is to be expected because one of the stimuli was presented in the visual field of the neuron. (3) The increase in the rate of response to the onset of the stimulus display was enhanced when the monkey was instructed to saccade to the stimulus in the visual field or attend to that stimulus, responding by releasing a bar when that stimulus dimmed, but continuing to hold the eyes focussed on the fixation point.

(4) No enhancement of the rate of response occurred when the monkey was instructed to attend to a stimulus outside of the visual field.

Because the stimulus display was the same in all four tasks, the explanation for the enhancement in two tasks (saccade to visual field stimulus, attend to visual field stimulus) must lie in the cognitive demands of the task, rather than the perceptual display. Because the enhancement occurred in two tasks that had different responses (saccade to visual field stimulus, attend to visual field stimulus), the enhancement must reflect an increase in neural responsiveness that is not tied to a single response system. Because the enhancement occurred when the monkey attended to the visual field stimulus but not when the monkey attended to the stimulus outside of the visual field, the enhancement must be selective for certain stimuli, rather than a general arousal response to all stimuli. This pattern of results leads to the conclusion stated above: attention to a stimulus can enhance the firing rate of cells in the Pdm, this enhancement is selective for that stimulus and is generalizable across at least two different response systems, saccadic eye movements and hand movements.

Together, the enhancement of neural response in the Pdm by attention to a visual stimulus, and the changes in attention produced by muscimol, suggests that the neural enhancement can have a potent influence on directing visual attention. The magnitude of a direct solictory effect cannot be determined because, unfortunately, a no-cue condition was not included. Consequently, only an indirect assessment can be made from the slowing of RT in the control condition for invalid trials as compared to valid

trials.

Focussing Attention On An Element In A Visual Display:
Pulvinar Activity Is Correlated With Attentional Demand

Detecting a target stimulus in a background of irrelevant stimuli is a more difficult task than detecting the same target by itself. When a target is embedded in display, attention must be used to separate the target from the rest of the display and enhance the processing of the target relative to the background. When the target is presented by itself, this selective attention is unnecessary because no distracting stimuli are present. Pulvinar cells increased their activity when the task required detecting a target in a background irrelevant stimuli as compared to a task in which the target was presented by itself. Because the pulvinar does not receive direct projections from sensory systems involved in this task, this pattern of results was interpreted as indicating that pulvinar neurons may be part of the neural system that is activated when visual attention must be focussed on an element in a display.

This experiment does not provide a strong test of the hypothesis that the pulvinar is involved in attention because an alternative explanation, emphasizing the physical properties of the stimuli, can explain experimental data. However, other experiments examining the psychological functions associated with the pulvinar have provided evidence for an attentional role. Consequently, the data from the present experiment can be considered as confirming

the conclusions from these other experiments, and providing weak support for the role of the pulvinar in attention. If the suggestions from the present experiment are accurate, then the pulvinar may have an important role as a mechanism directing selective attention. When the task demands are altered to increase the need for selective attention, the pulvinar may be activated to provide the mechanism for selection to occur.

The extent to which the pulvinar is required for selective attention, can be tested only with a lesion experiment. If the changes in neuronal activity described in the present recording experiment are required for selective attention, then lesions of the pulvinar should produce a major impairment in performance of tasks that require selective attention.

PARIETAL LOBE AND SHIFTING OF VISUAL SPATIAL ATTENTION

Shifting attention to a visual target in one visual field (left or right) normally involves parietal lobe function. Unilateral lesions of the parietal lobe, especially on the right side of the brain, substantially increased reaction time to a visual stimulus presented in the visual field contralateral to the lesion as compared to that same stimulus presented in the visual field ipsilateral to the lesion. The subject's task was to press a button as quickly as possible as soon as the visual target (an asterisk) appeared. At the beginning of each trial, a stimulus was presented to engage the person's attention. The target stimulus followed, and remained on until the person made a response. The

normal shift of attention to stimuli in the field ipsilateral to the lesion (ipsilateral field) coupled with the impaired ability to shift attention to stimuli in the visual field contralateral to the lesion (contralateral visual field) suggests that the parietal lesion caused a selective impairment for stimuli in the contralateral field as compared to the ipsilateral field, and this impairment was due to difficulty in shifting attention from an already attended stimulus to the stimulus in that field.

Valid cues directed the person's attention to the location where the target appeared. Consequently, no shift of attention between presentation of the cue and presentation of the target was necessary. Invalid cues directed attention away from the location of the target, towards the other visual field. Consequently, between the onset of the cue and the onset of the target, attention had to be shifted from the field indicated by the cue to the actual field in which the target occurred. If parietal lobe lesions impair the ability to shift attention into the contralateral visual field, then the patient's RT for the invalid trials should be much greater when the invalid cue was in the contralateral visual field and the target was in the ipsilateral visual field than with the opposite combination (invalid cue in the contralateral field and target in the ipsilateral field).

Validity, of course, should have a substantial effect by itself, even for normal subjects. Valid cues direct attention to the location at which the target appears, and thus should facilitate RT. In a complementary fashion, invalid cues direct attention away from the location in which the target appears, and

should disrupt RT. A main effect of validity is expected in any experimental procedure.

The important prediction for the patients with unilateral parietal lobe damage is for an interaction of the location of the cue and the magnitude of this validity effect. On invalid trials, shifting attention from the ipsilateral (normal) visual field to the contralateral (impaired) visual field should be very difficult, while shifting attention from the contralateral (impaired) visual field to the ipsilateral (normal) visual field should be relatively easy.

In summary, when the target is actually in the contralateral field, the validity effect should be very large; when the target is in the ipsilateral visual field, the validity effect should be relatively smaller.

The conclusions from this study are slightly complicated by the fact that data from a critical comparison procedure are absent. As outlined above, every trial in these experiments began with some kind of cue. Thus, although RT can be compared for targets in the different visual fields following a cue, no information is available for RT to targets when no cue preceded them. If parietal lesions do indeed produce a problem shifting attention to the target, then RT following parietal lesions should be normal if no shift is required. A sentence commented that RT to targets when no cue was presented was similar for targets in both visual fields, but no further information was provided, so that the procedure and results cannot be evaluated.

SELECTIVE AND DIVIDED ATTENTION

Selective attention to a single attribute of a stimulus, as compared to divided attention among all three attributes of a stimulus, activated some cortical areas as indicated by changes in PET. Attending to one attribute of a complex stimulus can enhance accuracy and speed responding to that attribute as compared to a condition in which attention is divided between the target attribute and other attributes. The magnitude of the enhancement is influenced by a variety of variables, including the difficulty of detecting the target attribute. The more difficult the detection, the greater the potential improvement in performance as a result of selective attention. The present study used an experimental design that presented visual stimuli that differed in shape, color, and velocity, and presented the same stimulus display with two sets of attentional instructions. In the selective attention task, the person was instructed to attend to only one attribute of the three, and the correct response was determined solely by the characteristics of the attended attribute. In the divided attention task, the person was instructed to pay attention to all three attributes, and the correct response could be determined by any one of the three. The selective attention condition, as compared to the divided attention condition, enhanced the activity of several cortical regions. Although the data analysis did not include the appropriate statistical tests to determine the selectivity of the effect, the results do lead to the conclusion that selective attention to stimulus attributes, just

like selective attention to a spatial locus, can alter neuronal activity in the cortex.

PET scans of blood flow were obtained in 9 people performing these tasks and also in a no-task condition in which they did not have to respond to the stimuli. For several areas in the extrastriate cortex, data are presented for normalized PET counts, which are linearly correlated with blood flow. For each of the single stimulus attributes (shape, color, velocity), these PET counts in the divided attention task were subtracted from those in the selective attention task. Positive differences indicate increased activity of cells in the area during the selective attention task, a result demonstrating that selective attention, relative to divided attention, enhanced activity in this area.

Areas in which selective attention enhanced PET counts included: lingual gyrus, fusiform gyrus, parahippocampal gyrus, parietal-occipital sulcus, superior temporal sulcus, inferior parietal lobe, dorsolateral occipital cortex.

Unfortunately, two characteristics of the report limit interpretation of the results. First, data are not available for every area in every task. Second, no analysis of variance was conducted on the differences among the differences (the differences between brain areas for the magnitude of the difference between the selective attention and the divided attention condition). Consequently, no conclusions can be made about the selectivity of these changes, e.g. the extent to which attention to a given stimulus attribute differentially altered activity in some brain regions as compared to others.

In conclusion, selective attention to a stimulus attribute, as compared to divided attention among attributes, can enhance activity in many cortical areas. This enhanced activity is a neuronal correlate of the enhanced sensitivity in detecting changes in the visual stimuli. The neuronal changes are widespread, affecting many neural structures, and conclusions about the specificity of the effect cannot be drawn from the current set of data.

Divided Attention, Frontal cortex and the
Nucleus Basalis Magnocellularis

The nucleus basalis magnocellularis (NBM) has been linked to attentional processes by studies using lesion and recording techniques. Lesions of the NBM impaired divided attention. In one study, rats were trained to discriminate two different signals; each signal was associated with a different fixed interval. Focused attention was assessed by presenting one stimulus. Divided attention was assessed by presenting both stimuli simultaneously. Normal rats accurately timed each of two stimuli whether they were presented alone or together, demonstrating good focused and divided attention. Rats with lesions of the NBM or frontal cortex were able to time each stimulus when it was presented alone, but not when it was presented with the other stimulus, demonstrating an impairment of divided attention. Because the NBM sends cholinergic fibers to the frontal cortex, the results suggest that the cholinergic neurons originating in the NBM and projecting to the

frontal cortex are important in divided attention.

A second study using electrophysiological recordings from the frontal cortex provides supporting evidence that this brain region is important in divided attention. Electrophysiological recordings were obtained from 123 neurons in the frontal cortex while rats performed a divided attention task. Each rat was trained to discriminate between two stimuli, each associated with a different fixed interval. Focused attention was assessed by presenting a single stimulus. Divided attention was assessed by presenting both stimuli together. Neurons in the frontal cortex had four patterns of activity. (1) "Divided attention" neurons responded more when both stimuli were presented than when a single stimulus was presented. These results, together with results following lesions of the frontal cortex, suggest that the frontal cortex is important in divided attention. (2) "Selective attention" neurons responded to each stimulus when presented alone, but responded to only one stimulus when both stimuli were presented together. These cells may be important in selective attention. (3) "Single task" neurons responded to only a single stimulus, when presented alone and in conjunction with the other stimulus. These cells may be involved in processing of a single task, regardless of whether a second task is also being processed. (4) "Lever press" neurons had responses that were closely associated with lever press rate. In summary, neurons in the frontal cortex are activated by different aspects of the temporal discrimination task, including divided and selective attention.

DYSFUNCTION OF ATTENTION

The parietal lobe is involved in visual spatial attention. Following unilateral parietal lobe lesions subjects report unilateral neglect for the contralateral visual field. These results have been interpreted as a dysfunction of visual spatial attention because early visual evoked potentials are normal in the normal hemisphere. These early evoked potentials probably arise from visual cortex in the occipital lobe, and indicate that subjects are not blind and do receive the visual information at least to the point of visual cortex. Further evidence that the neglect is not perceptual comes from a milder version of unilateral neglect, called extinction. Patients with a unilateral lesion of the parietal lobe will respond to a single stimulus when presented in either visual field, but when two stimuli are presented each in a different visual field, the stimulus in the good visual field is the only stimulus that elicits a response. In extinction, the subject can not be blind to objects presented in the contralesion visual field; when a single stimulus is presented in the contralesion visual field, the subject can respond to it. The second source of evidence suggesting the parietal lobe is important in visual-spatial attention comes from neurophysiological studies. Many neurons in the parietal lobe are activated by visual stimuli. Visual fields can be mapped out for these neurons and they occur in the contralateral visual field. In addition, the firing characteristics of these neurons are modulated by attentional factors. Enhancement of firing rate occurs when a stimulus is

presented in the receptive field and under conditions when that stimulus is an important stimulus for a response. Enhancement occurs in parietal lobe neurons when the stimulus presented in the receptive field is a target for saccades or is a signal to make a hand response. The enhancement of firing rate in parietal lobe neurons is spatially selective, i.e., enhancement occurs only when the target stimulus is in the neuron's receptive field. The enhancement in parietal lobe neurons is not response specific, and occurs in tasks where a saccade is to be made or when a hand movement is to be made. The critical feature that appears to be important in eliciting enhancement is the direction of attention to a stimulus in the neurons receptive field. Both the lesion and the electrophysiological data point to an important role of the parietal lobe in visual spatial attention.

The results from patients with unilateral lesions of the parietal lobe suggest that the parietal lobe is involved in spatial attention for nonvisual modalities as well. Subjects with unilateral parietal lobe lesions have unilateral neglect for somatosensory stimuli as well as auditory stimuli. What needs to be researched in this field is whether unilateral neglect for somatosensory and auditory stimuli always occur together with unilateral neglect for visual stimuli. If unilateral neglect occurs for all three modalities following lesions of the parietal lobe, the parietal lobe must be involved in spatial attention for many modalities. Even if the unilateral neglect for the three modalities is not 100% correlated, different regions of the parietal lobe may be involved in spatial attention for each

modality. The same neurons may be responsible for spatial attention of all three modalities, or one set of neurons may be important for visual spatial attention, another for somatosensory spatial attention, and a third for auditory spatial attention.

The responsiveness of parietal neurons to nonvisual stimuli has not been studied extensively. Parietal neurons are activated by both visual and somatosensory stimuli. These neurons are located in the ventral intraparietal area (VIP). The VIP area sends projections to areas MT and MST, the motion sensitive regions of the superior temporal sulcus. All neurons in area VIP had visual receptive fields. These neurons are responsive to a wide variety of visual stimuli and are very sensitive to stimulus motion. In these respects, the properties of VIP neurons are similar to those of cells in MT and MST. Some neurons are sensitive to the direction of motion of the stimulus, stimulus depth, and speed of movement through the receptive field.

Attention modulates the activity of neurons in the VIP area. Enhancement of activity occurs when a stimulus is presented in the neuron's receptive field, and when the stimulus is a target for a saccade. If these neurons behave similarly to those neurons described in previous studies, then the activity of these neurons should be enhanced in a nonsaccade test in which the stimulus is a signal for the animal to make a hand movement response. These properties have previously been described for neurons located in the parietal lobe. The unusual feature of these cells is their responsiveness to somatosensory stimuli, with the somatosensory receptive field and the visual receptive fields having similar

properties: spatial location, field size, and motion selectivity. For example, a neuron with a visual receptive field in the upper contralateral quadrant of visual space may have a somatosensory receptive field in the contralateral upper quadrant of the face and above the ear. The vertical meridian of the visual field matches the body midline, the visual field horizontal meridian matches a line in the somatosensory field which bisects the face, and the eccentricity of the visual receptive field matches the deviation of the somatosensory receptive field from the midsagittal plane (for example, cells with frontal somatosensory receptive fields have more central visual receptive fields). The sizes of visual and somatosensory receptive fields are also correlated so that cells with small visual receptive fields have small somatosensory receptive fields and cells with large visual receptive fields have large somatosensory receptive fields. Finally, the directional sensitivity of these cells is correlated in the visual and somatosensory modality.

THE ELEMENT SUPERIORITY EFFECT: ATTENTION?

A series of experiments with pigeons have used a variation of the match-to-sample procedure to demonstrate that the characteristics of the sample can affect performance during the subsequent choice test, and have interpreted these differences in performance as reflecting differences in attention. However, this interpretation has been challenged recently. Because these experiments have been an important line of research using concepts

of attention to describe the performance of animals, they will be reviewed briefly here, describing in order the concept behind the experiments, the basic procedure and results, and the recent problems in interpretation.

If the ability to process stimuli is limited, then the rate at which information can be obtained about a given stimulus should depend on the complexity of that stimulus. In the context of the present experiment, this hypothesis leads to the prediction that performance during a test should be better (choice accuracy higher, reaction time shorter) if the stimulus to be remembered has a single dimension identifying it, rather than two or more. The term "element superiority effect" refers to the fact that in the basic experimental procedures, a sample stimulus with a single element produces better performance than a compound stimulus with two elements.

The typical experimental procedure requires the animal to respond to one of two test stimuli, with the test stimulus that is correct being determined by the characteristics of the sample stimulus presented immediately prior to the test stimuli. The type of sample stimulus differed in the two types of trials. For element trials, the sample stimulus had only one dimension, whereas for compound trials, the sample stimulus had two dimensions. On element trials, the stimulus might have the dimension of shape (square or triangle) or color (red or blue), but not both. For compound trials, the stimulus had both dimensions, one shape and one color. For the test trials, the two stimuli had only one dimension: one stimulus had one value, the other stimulus had a

second value.

The element superiority effect appears as better performance on test trials following element stimuli than following compound stimuli. Thus, when the pigeon was given only one relevant dimension to remember (either shape or color), performance was better than when two relevant dimensions (shape and color) were present. The limited capacity attentional explanation interprets these data as follows. Encoding the information from the sample stimulus requires cognitive capacity. This capacity is limited. Encoding two dimensions of a stimulus is more difficult than encoding a single dimension.

Although this interpretation is adequate to describe the basic element superiority effect, it fails to explain the results obtained from two variations from this effect. One variation tests the hypothesis that the magnitude of the element superiority effect should decrease as the duration of the sample stimulus is increased. If the element superiority effect with brief presentations of the sample is due to limited encoding capacity, long presentations of the sample stimulus should remove that capacity limitation, and allow accurate encoding of all information in the stimulus. The experimental procedure is the basic one as described above with both compound and element stimuli, with the additional variation of the duration of the sample stimulus. The limited capacity attentional hypothesis of the element superiority effect predicts an interaction of the magnitude of the element superiority effect and the duration of the sample stimulus, this magnitude decreasing with increased stimulus duration.

Unfortunately, for the hypothesis, this interaction does not occur.

A second problem for the limited capacity attentional hypothesis of the element superiority effect is the presence of an interaction of performance with the duration of the test stimulus. These particular experiments were conducted with humans, rather than pigeons. Consequently, the possibility must be left open that experiments with pigeons may not demonstrate the interaction described here. However, all other aspects of performance in the relevant experiments were similar for pigeons and humans. Therefore, the most likely outcome to predict in the experiments with pigeons is the same pattern of results as in the experiments with humans.

The experimental design was the same as that described above for the interaction with the duration of the sample stimulus except that the duration of the test stimulus was manipulated. The sample stimulus was 100 msec. The test stimulus was either 100 msec or 500 msec. With the short (100 msec) test stimulus, the element superiority effect occurred; reaction time for trials with element stimuli was faster than reaction time for trials with compound stimuli. With the long (500 msec) test stimulus, the magnitude of the element superiority effect was greatly reduced, producing the statistical interaction between the duration of the test stimulus and the type of sample stimulus.

Together, these results demonstrate that the relevant cognitive mechanisms are not active at the time of the sample stimulus, but are active at the time of the test stimulus. Consequently, attentional interpretations emphasizing a limited

capacity for encoding information about the test stimulus must be incorrect. Rather, alternative explanations focussing on cognitive mechanisms responsible for comparison of the test stimuli to the sample stimulus and making an appropriate response must be the important variable.

In summary, the element superiority effect is important for three reasons. (1) It has been the subject of substantial investigation in animals and has produced a large body of literature that has been interpreted in terms of attentional mechanisms. (2) It is one of the few tests of attention that has been given to both humans and nonhuman animals. (3) The attentional interpretation of this phenomenon has recently been questioned.

ANIMAL MODELS OF ATTENTION DEFICIT

Animal models of attention deficit have been pursued for several reasons because they are critical to describe and understand the neural machinery that is involved in attentional processes, and because they can help investigate the clinical syndromes that are thought to involve impairments in attention. Two noteworthy dysfunctions are schizophrenia and attention deficit hyperactivity disorder (ADHD). These disorders may encompass a number of other cognitive deficits, but many theories focus on the attentional deficits. Good animal models of attentional deficits are useful and facilitate the development of therapeutic approaches to treating these diseases.

Latent inhibition is the detrimental effect of passive, nonreinforced exposure to a stimulus on the subsequent ability to form new associations to that stimulus. This phenomenon has important implications for the study of attention because the process of latent inhibition changes the relative ability of stimuli to alter behavior, and has often been interpreted in terms of an attentional mechanism. An excellent and recent review is available in Lubow, 1990, and the reader who is interested in the details of this analysis is encouraged to consult that reference for further information. The present discussion will focus on only those aspects of latent inhibition that are most relevant to the analysis here.

The assessment of latent inhibition (LI) has been used for a number of years to measure attention in animals. Recently, the LI procedure has been used in schizophrenic patients. The similar results found in schizophrenic patients and animals given amphetamine has provided evidence that the LI procedure may be a valid model of attention deficits.

The basic design for an experiment to demonstrate latent inhibition has three components. (1) An experimental group, as compared to a control group, is presented with a stimulus. (2) Subsequently, both groups are given a conditioning procedure to learn to associate the stimulus presented in phase 1 with some event. (3) Latent inhibition is demonstrated by impaired acquisition of the new association in the experimental group.

The LI procedure presents a stimulus without any reinforcement contingencies. During the conditioning phase that follows the

exposure phase, the same stimulus is paired with a reinforcer. The ability to learn the association between the stimulus and reinforcer is measured. In normal subjects, exposure of the stimulus inhibits learning the association of the stimulus and reinforcer. One explanation is that during the exposure phase, the subjects learn that the stimulus does not predict reinforcement. The stimulus is coded as irrelevant and is therefore ignored. Because the stimulus is ignored, the association between stimulus and reinforcer is acquired slowly during the conditioning phase. This retardation of learning due to exposure is termed latent inhibition. Subjects with attention deficits learn the association between stimulus and reinforcement during the conditioning phase faster than normal subjects. Here, the explanation is that attention deficits prevent these subjects from filtering out the irrelevant stimulus. Therefore, during the conditioning phase, the stimulus is not ignored and is readily associated with the reinforcement.

Recent data have implicated the nucleus accumbens as an important brain structure in latent inhibition. Amphetamine, which produces symptoms of acute schizophrenia, reduces latent inhibition. This effect of amphetamine can be abolished by lesions of the nucleus accumbens. Additional evidence for a role of the accumbens in latent inhibition is that lesions of the ventral hippocampus and subiculum block latent inhibition and these structures project to the same cells in the accumbens that receive input from the mesolimbic dopaminergic system. In humans, schizophrenics exhibiting Type 1 symptoms have reduced latent

inhibition compared to controls reduced numbers of cells in the accumbens. These results suggest that the accumbens is important in attention and may be one of the neurobiological dysfunctions involved in the attentional deficits of schizophrenics.

One obvious difference between the experiments using the procedure of latent inhibition with animals, and those studying selective attention in humans, is the time course of the manipulation and the measurement. In experiments that measure reaction time in humans, the independent variable that manipulates attention is often very brief, a verbal instruction, a few minutes of experience, or a cue that is present for only a few hundred milliseconds. Likewise, the effect of the independent variable is usually immediate, seen in the first few trials. In contrast, the manipulation to produce latent inhibition in animals typically uses many trials, and the measurement of its effect also takes place during many trials. As pointed out previously, however, definitions of selective attention have generally not placed a time parameter on the effects, and an analysis of the neural mechanisms may be required to determine whether short-term plasticity (both manipulations and effects) and long-term plasticity (again, both manipulations and effects) use different mechanisms or not.

In short, latent inhibition is an important phenomenon in itself, and has had a significant impact on thinking about attentional processes in animals. In addition, a comparison of the procedures and results used in latent inhibition with those used in typical reaction time experiments highlights many of the issues concerning the mechanisms controlling attention, and the ways in

which attention should be distinguished from other forms of plasticity.

CONDITIONED ATTENTION THEORY

Latent inhibition, and the theoretical description of this phenomenon in conditioned attention theory (CAT), are important because the phenomena and the theory suggest that the ability of a stimulus to be associated with another stimulus is a function of the amount of attention given to that stimulus. By implication, all the phenomena of conditioning are modified by attentional processes. If such is the case, CAT has profound implications for the understanding of many different types of behavior and the cognitive processes underlying these.

A recent theoretical analysis of latent inhibition is provided by Lubow (1989) in his discussion of conditioned attention theory (CAT). CAT is designed to incorporate all the basic phenomena of latent inhibition, organize these in a coherent theoretical framework, and indicate the ways in which latent inhibition can be placed within the framework of classical conditioning.

CAT "...states that nonreinforced exposure to a stimulus retards subsequent conditioning to that stimulus because during such pre-exposure the animal learns not to attend to it. The theory is based on the use of attention as a hypothetical construct, with the characteristics of a Pavlovian response, and on the specification of reinforcement conditions that modify intention." (Lubow, 1989, page 190). In the discussion that

follows, the importance of the amount of attention given to a stimulus should be always kept in mind. The discussion will mainly describe the experimental data and theory in terms of the amount of attention. However, attention, in turn, has a profound effect on the associability of events with a given stimulus. Consequently, changes in attention have a substantial influence on the extent to which the stimulus in question enters into associations through conditioning. Greater attention leads to greater associability.

A continuum of attention is postulated by CAT. Thus, attention and inattention are treated as two ends of a single process, rather than as two different processes. The empirical laws of conditioning are postulated to influence attention (Lubow, 1989, Page 196-205.) Attention is treated like any other response that is altered by classical conditioning, and influenced by the variables already identified as influential in classical conditioning. These are stated explicitly in terms of latent inhibition, but because latent inhibition is a form of conditioned inattention, they can be restated in terms of conditioned inattention.

Conditioned inattention is:

1. Relatively long-lasting.
2. Specific to a stimulus.
3. A positive function of the number of times that a stimulus has been presented without reinforcement.
4. A positive function of the time between stimulus presentation.
5. A positive function of stimulus intensity.
6. Influenced by external inhibition, i.e. distraction.

7. Influenced by blocking.
8. Influenced by overshadowing.
9. Subject to extinction and spontaneous recovery.
10. Enhanced as a result of adaptation to other stimuli.

Considering attention as a conditioned response may seem to be an unusual approach. However, it is not significantly different than the usual view of attention as a property of the information processing system. In both views, attention can be manipulated, and that is the critical feature that allows CAT and other views of attention to be related to each other. Indeed, the whole point of CAT is that a powerful theoretical framework, in the form of conditioning, can be brought to understand some of the variables that influence attention and some of the effects of attention. In describing attention as a response, CAT clearly does not mean to imply that it is at the motoric periphery of the cognitive process or the individual. Rather, this response is sufficiently central to have a profound influence on subsequent processing of stimulus information. As such, the basic idea of CAT is clearly compatible with other approaches that do not consider attention as a response.

The analysis provided by CAT is important for two reasons. (1) It provides a coherent approach to a phenomenon, latent inhibition, that has been intensely examined experimentally, and has been described theoretically in the framework of attention. CAT is currently the most comprehensive analysis of this phenomenon, and offers a coherent theoretical framework to understand it. (2) Neural analyses of attentional processes are possible within the context of latent inhibition. To the extent

that latent inhibition and CAT provide a useful analysis of some forms of attention, these experimental procedures in theoretical frameworks can be adopted to identify the neural systems involved in attention. Considerable work has provided information about the role of accumbens in latent inhibition, with experimental procedures that can systematically be adapted to answer many other questions in attention. An extension of the techniques (single unit recordings, lesions, intracranial infusions, etc.), anatomical structures (frontal cortex, basal forebrain cholinergic system, dopamine) and theoretical frameworks (especially analyses directed to the site of change of stimulus processing and the site that produces this change) could be particularly powerful. As stated previously, one intended goal of this report is to stimulate an integration of different approaches to attention, and latent inhibition, in the context of CAT, offers an excellent opportunity.

NEUROBIOLOGY OF ATTENTION

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NEUROBIOLOGY OF ATTENTION

BIBLIOGRAPHY BY SELECTED TOPICS

Aging

Audition

Evoked Related Potentials

Frontal Cortex

Catecholamines

Parietal Lobe

Schizophrenia

Sensory Neglect

Vision

Somatosensory

Aging

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NEUROBIOLOGY OF ATTENTION

BIBLIOGRAPHY OF SELECTED TOPICS

Aging and Alzheimer's Disease

Audition

Computational Models

Event Related Potentials

Frontal Cortex

Lateral Hypothalamus and Motivation

Noradrenergic System

Nucleus Accumbens

Parietal Lobes

Parietal Lobe Electrophysiology

Reticular Formation

Schizophrenia

Sensory Neglect

Somatosensory

Vision

Vision-Electrophysiology

Brain Mechanisms and Attention

Aging
Audition
Computational Models
Event-Related Potentials
Frontal Cortex
General
Lateral Hypothalamus and Motivation
Noradrenergic Function
Nucleus Accumbens
Parietal Lobes
Reticular Formation
Schizophrenia
Sensory Neglect
Somatosensory
Vision

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13

Attention: Neurocognitive Analyses

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Both neural and cognitive systems have considerable plasticity. The same stimulus at different times may elicit different responses depending on the influence of other variables on the system. The characteristics of this plasticity differ markedly in terms of many parameters: the variables that produce it, how quickly it occurs, how long it lasts, what stimulus and response systems can be influenced, and so forth.

The major purpose of this chapter is to compare analyses of plasticity that have been conducted in the context of memory and attention, with the primary goal of suggesting ways in which lessons learned from the analysis of the brain mechanisms involved in mnemonic processes can be applied to the analysis of the brain mechanisms involved in attentional processes. Riley has made substantial contributions in the analysis of both memory and attention. Our approach builds on those contributions, relying heavily on the ways in which cognitive processes can be analyzed in animals, and extending that approach to the integration of neural and cognitive analyses of psychological processes.

COMPARATIVE COGNITION

Although comparative cognition is used most often as a term to describe comparisons between different species, it is also appropriate for the comparison of two individuals within the same species because these individuals may differ substantially in their neural mechanisms, genetic background, experience, or other variables that may influence cognitive processing. Historically, the discussion of comparative cognition often has begun with a substantial bias toward one partic-

ular view of the extent to which the individuals being compared are similar or different. This bias may reflect a particular view of evolution, species, cognitive processes (especially language), genetic background, or any other influential variable. A major contribution of the recent developments in comparative cognition is to provide a theoretical and experimental basis to choose empirically among the many different alternative explanations of the differences among individuals. The general issues involved in comparative cognition have been discussed extensively elsewhere, both by Riley and by others, and are not reviewed here (Riley, Brown, & Yoerg, 1986; Roitblat, 1987). Rather, the emphasis is placed on the application of this approach to the analysis of plasticity in memory and attention, with special emphasis on the importance of comparative cognition to determine the neural mechanisms underlying cognitive processes.

For the understanding of neural mechanisms involved in cognitive processes, comparative research with animals is important for two reasons. First, the brains of animals differ substantially in many characteristics, suggesting that some of the neural mechanisms involved in a given cognitive process must differ from one species to the next. For example, the hippocampus of both mammals and birds is involved in memory, but the gross structure of the hippocampus, and its cellular organization are substantially different in the two species (Olton, 1989; Sherry & Vaccarino, 1989; Sherry, Vaccarino, Buckenham, & Herz, 1989). An appreciation of the ways in which the similarities and differences of this brain area contribute to the similarities and differences in memory between the two species is critical to determine the ways in which neural systems can mediate memory. Many characteristics of the brain vary substantially across species. Consequently, any attempt to describe the general principles involved in the neural mechanisms of cognitive processes must include a comparative approach to encompass this variability.

A second reason for using comparative approach to study cognitive processes in animals is to obtain general principles that may hold for the neural mechanisms of cognitive processes in several species of animals, including humans. Direct access to human brain, both to manipulate it and measure it, is extremely limited, both in current practice and in the foreseeable future. As long as the welfare of the individual being studied is more important than the acquisition of basic knowledge (an ethical position that is so strongly developed that it is unlikely to change), detailed information about the neural systems involved in human cognition cannot be obtained in sufficient detail to resolve fundamental issues about the relation between mind and brain. The focus of this chapter is on this second approach, the use of animals to identify the general neural mechanisms involved in cognitive process such as memory and attention.

MEMORY

The integration of comparative cognition and neural analyses to understand the neural systems involved in memory in humans is well established. An empirical

indicator of the extent to which the analysis of memory has been integrated between humans and other mammalian species is the number of cross-references in articles using one species to data obtained from other species. Information about the three mammalian species most often tested (rats, monkeys, and humans) is frequently brought together to address important issues concerning the neural mechanisms of memory. For example, recent memory in rats, monkeys, and humans is impaired following lesions of the hippocampus. These results suggest a common function of the hippocampus across species. This conclusion could be obtained only by the free exchange of information between investigators studying recent memory in the different species. This free interchange of information may both reflect the benefits of a comparative approach, and be a catalyst to stimulate it. Once this interaction is begun, of course, it often continues easily and may be refined to allow even further integration. This article suggests that the steps taken to integrate studies of the neural mechanisms of mnemonic processes may be beneficial to produce a similar integration of the neural mechanisms of attentional processes, and develops this line of thought by first reviewing the relevant information in memory, and then extending the principles to the analysis of attention.

The term model has been used often when examining memory in animals. Sometimes, this term is appropriate in the sense that the procedure is designed to replicate that used in a human. In other cases, it is probably inappropriate because the memory process itself is of direct interest, whether or not it has been studied in humans. The term model often implies that a particular standard is the only criterion for being correct. This attitude is inappropriate in most analyses of comparative cognition because each analysis may be legitimate in its own right. For the present discussion, the major purpose is to analyze the commonalities in memory across different mammalian species, particularly, humans, rats, and monkeys. In this context, the goal is to provide accurate assessment of a particular memory process in all three species rather than to adopt a particular procedure used for a particular species as a model for the other species.

To provide some specific examples of the general points raised in this discussion, consider the analysis of recent memory in mammals. Recent memory involves the recall of previously presented information, usually maintaining it within a specific context or episode. It is often assessed by some specific variation of a delayed conditional discrimination. In this type of discrimination, some information is presented to the individual at the beginning of the trial. After a delay, two or more response alternatives are made available, and the response that is correct depends on the information that was presented at the beginning of the trial. In humans, recent memory can be assessed in many ways; some examples include reading a specific story and asking for recall of it as in the Wechsler Adult Intelligence Scale, or by presenting three specific nouns and asking for recall of them as in the "Mini-Mental" test (Folstein, Folstein, & McHugh, 1975). In animals, some version of a match to sample or nonmatch to sample is often used. For example, in an operant box, the stimulus might be either a red or

green circle, and the response might be pressing a lever under either a black square or a black triangle. For a symbolic match-to-sample test, a response to the black square is correct following the red circle as the stimulus; a response to the black triangle is correct following a green stimulus.

An important step in the integration of studies from humans and nonhuman mammals has been the development of nonverbal tests of recent memory for humans (Bartus & Dean, 1981; Freedman & Oscar-Berman, 1986; Kesner, Adelstein, & Crutcher, 1987; Olton, 1990b; Wright, 1989). A comparison of the results from these nonverbal tests in humans with those from the verbal tests in humans and with the nonverbal tests in animals can assess the generality of the conclusions drawn from experiments with verbal material in humans. Again, the ability to adapt procedures across different species, without giving primacy to any one given test in any one given species, is an important step in integrating the relevant information (Wright, 1989).

Indeed, a major contribution of comparative cognition has been to emphasize the importance of abstract cognitive and computational analyses that are conducted independently of particular test procedures. A complication in any comparative analysis arises when the concepts or data used for comparison are tied so closely to a particular experimental procedure that the only way to test the generality of results from one species to another is to replicate the procedure exactly. A fundamental goal in assessing cognitive processes is to provide multiple, converging operations so that variables influencing the empirical processes of manipulation and measurement can be separated from those influencing the primary cognitive process being studied (Garner, Hake, & Erickson, 1956; Olton, 1990a; Platt, 1964; Rescorla, 1988; Waldorf, 1990a, 1990b).

The comparison across mammalian species for analyses of recent memory has been subject to considerable discussion, often in the context of animal models of procedures used for humans. The measurement of normal memory in humans, and the description of the amnesic syndromes following different types of brain damage, has been extensive, and has stimulated considerable research with animals. Conferences, books, and articles typically include references to four different areas: experimental psychology (memory in normal humans), clinical neuropsychology (amnesic syndromes in patients), comparative cognition (memory in animals), and physiological psychology (the brain mechanisms involved in memory). This continued cross-fertilization has led to considerable agreement about the criteria and dimensions that should be used to compare analyses and memory in different species.

Independent Variables. The demand on recent memory can be manipulated parametrically by altering the *task demand*, the extent to which a particular component of a task is required for successful performance (Olton, 1989). Task demand for recent memory can be manipulated by procedures that alter interference among the items to be remembered. Several empirical manipulations are commonly used. The first is increasing the delay/retention interval between presentation of the stimuli and the opportunity to make responses. The longer

260/28

this delay interval, the greater the demand on recent memory, the worse the performance following the delay. The second manipulation is the number of items to be remembered. The greater the number of items presented as sample stimuli at the beginning of the trial, the greater the demand on recent memory, the worse the performance following the delay. The context in which a given stimulus is presented can have a marked effect on the ability to recall that stimulus. Both the type of trials preceding the current one, and the temporal intervals in all of the components of the test session, not just the current trial, may influence interference, and choice accuracy. For example, choice accuracy on the current trial with a given delay and a different correct response than on the previous trial may be greater if the intertrial interval is longer, rather than shorter, because the longer interval reduces interference from the previous trial. Interference may be produced by stimuli and responses, and probably other components of the trial (Olton & Shapiro, 1992).

In summary, comparative analyses of the neural and cognitive mechanisms involved in recent memory are helped immensely by agreement on the parametric variables that can be used to manipulate task demand for recent memory. These are sufficiently empirical to reach consensus about what should be done in a given experiment, yet sufficiently general that the actual manipulations are easily adapted to testing with any given species.

Conceptual Framework. Considerable discussion concerns the appropriate taxonomic categorization of memory, and many different theoretical frameworks have been suggested. Although many of the disagreements are substantial and require resolution to provide a complete analysis of mnemonic processes, sufficient agreement is available that an appropriate conceptual framework for the analysis of recent memory can proceed. For example, both proactive and retroactive interference are present in recent memory. Proactive interference is the disruptive effect of previously presented information on the ability to remember currently presented information. Retroactive interference is the disruptive effect of currently presented information on the ability to remember previously presented information. Serial order effects are also present in recent memory. Primacy and recency, respectively, refer to the more accurate memory for items at the beginning and end of a list than for items in the middle. Tests of recent memory in different species can be compared on the extent to which these different psychological processes are involved (Wright, 1989).

In summary, in addition to the empirical manipulations of recent memory described in the previous section, theoretical descriptions of recent memory also can be used for comparative purposes. The agreement on the kinds of cognitive processes that should be observed in recent memory permits assessment of the effectiveness of manipulations of independent variables on the desired cognitive processes.

Evolutionary Factors. When searching for food, animals can use many different strategies. Discussions of optimal foraging have identified strategies that

vary in the extent to which they require recent memory. Both birds and rodents have been studied in the natural habitat to determine the extent to which recent memory guides their behavior. For example, some birds hoard food by placing seeds in a cache for a short period of time to hide the food, and then return to obtain it. This behavior is similar to that in an experimentally controlled delayed conditional discrimination, and these birds use recent memory to find their food. In contrast, other birds do not store food in caches, and use other kinds of strategies to obtain it. Similar differences exist among rodents. These analyses are important because they demonstrate that the natural habitat for an animal can put demands on recent memory, and that the types of procedures used to assess recent memory in laboratory tests can involve naturally occurring foraging strategies rather than being some unnatural never-before-experienced challenge to memory (Kamil & Balda, 1985; Sherry, 1984; Shettleworth, 1985). Involvement of the hippocampus in natural foraging as well as in laboratory tests of recent memory provides additional evidence that laboratory procedures can elicit natural mnemonic processes (Harvey & Krebs, 1990; Krebs, Sherry, Healy, Perry, & Vaccarino, 1989; Sherry & Vaccarino, 1989; Sherry et al., 1989).

ATTENTION

Several model systems have been developed to assess the neural basis of specific kinds of attention. However, no large-scale integration of the neural analysis of attention has yet been undertaken. As one indicator of the difference in the maturity of neural analyses of memory and of attention, consider the presentations at the Society of Neuroscience in 1991. In the slide and poster sessions, 21 were titled "learning and memory," and these had subheadings referring to electrophysiology, anatomy, neurochemistry, and other topics. No single session was labeled "attention." In the list of keywords, many presentations had the word *learning* or *memory* listed, whereas only a few had the word *attention* listed. Presentations at the Society for Neuroscience are not the only criteria to judge the amount of work being done in a given area, but even if these data are biased for some unknown reason, they demonstrate such a substantial difference that even significant quantitative adjustments would not change the picture. The point is clear: Much more research is being conducted on the neural analysis of mnemonic plasticity than on the neural analysis of attentional plasticity.

The reasons for this difference may be many, but one important difference in the study of memory and attention is the availability of experimental procedures for animals to assess attentional processes in ways that are homologous to those used in humans. In the study of attention, no analysis equivalent to recent memory, with appropriate independent variables, psychological constructs, and ethological considerations, has yet been developed. The seminal work of Riley and colleagues has made an important step in this direction, showing how an approach using the principles of comparative cognition can be applied to the

PANG

study of attention in animals (Bond & Riley, 1991; Brown, Cook, Lamb, & Riley, 1984; Riley, 1976; Riley & Leith, 1976; Riley & Roitblat, 1976). The object of the research program that we have just begun is to extend the analysis of attention and develop procedures that can be used for rats and that incorporate the same features used in experiments for humans. If tests of attention in humans and rats can be integrated in the same way that tests of memory have been integrated, then the rich conceptual and empirical body of information developed in the study of human attention can be applied to the study of attention in animals, which then opens the door to an examination of the neural bases of these attentional mechanisms.

EXPECTANCY AND ATTENTION

Expectancy is preparation for a specific event. If the expectancy is accurate and the event occurs, responding can be more rapid and more accurate (Hick, 1952; Hyman, 1953). The conceptual framework to describe the cognitive processes involved in expectancy have been developed primarily in analyses of the performance of humans in choice reaction time tasks. For the same reasons outlined previously in the study of memory, facilitation of the comparative analysis to examine the brain mechanisms involved in expectancy can be accomplished by using experimental procedures that have the same conceptual framework, operational procedures, and independent variables in both animals and people. The experiment described here was a first attempt to begin that unification of procedures (Pang, Merkel, Egeth, & Olton, 1992).

Conceptually, the experiment was designed to examine the effects of expectancy on information processing. As described previously, accurate expectancy for an event should facilitate responding to that event, decreasing reaction time, and increasing choice accuracy. The independent variable was the relative probability of two stimulus/response events within each test session. The dependent variables included reaction time, choice accuracy, discriminability, and bias. The procedures used variations of a two-choice reaction time task. For the rats, the procedures were made as similar as possible to those used in previous experiments with people. For humans, the procedures were as similar as possible to those used for the rats including the minor variations that were necessary to train the rats in the task. The procedures for the two species were identical except for three components: the increased amount of training given to the rats prior to testing, an explicit water reinforcement given to the rats but not the humans, and the specific equipment used for the testing.

For both species, a trial was initiated by depressing two response keys. After a variable delay, one of two stimuli, a tone or a light, was presented. For the light, lifting one response key was correct. For the tone, lifting the other response key was correct. Within each session, the probability of the two stimuli remained constant. Across sessions, these probabilities varied: (probability of light/prob-

ability of tone): 100/0, 90/10, 50/50, 10/90, 0/100. Reaction time and choice accuracy were measured, and discriminability and bias were calculated.

The predictions were as follows. If the probability of a stimulus within a session alters expectancy, responses to the expected stimulus should be faster and more accurate, producing a bias toward the expected stimulus. If rats, like humans, respond to changes in stimulus probability by altering expectancy, and expectancy has similar effects on information processing, then the pattern of results for rats should be similar to those for humans.

The pattern of results was similar to that predicted. As the probability of a specific stimulus increased, reaction time decreased, choice accuracy increased, response bias increased, and discriminability did not change. This pattern was similar for both rats and humans, with one exception: For rats, expectancy had little effect on responses to the auditory stimulus.

NEURAL MECHANISMS OF ATTENTION

The success of this comparative approach in the study of attention offers the opportunity to pursue neural analyses of attention in the same way that the neural analyses of memory have been developed. With conceptual and operational similarity in the approaches taken for the two species, additional behavioral experiments can be designed to test the extent to which rats and humans use similar cognitive mechanisms for other types of attentional processes, and then the neural bases of these can be examined.

The cholinergic projections from the nucleus basalis magnocellularis (NBM) to the frontal cortex may have an important influence on some types of attention. Lesions in this system disrupted divided attention for the temporal discrimination of two stimuli (Olton, Wenk, Church, & Meck, 1988; Olton, Wenk, & Markowska, 1991). Changes in the cholinergic innervation of cortical areas altered receptive fields to somatosensory stimuli (Dykes, Tremblay, Warren, & Bear, 1991). Microinfusion of drugs that altered cholinergic activity in the NBM altered attentional processes for stimuli in the procedures described here. The cingulate cortex also may be involved in certain types of divided attention as indicated by scanning with positron emission tomography (PET) in humans (Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). Other analyses have emphasized specific types of attention, such as visual attention related to eye movements and spatial location (Spitzer, Desimone, & Moran, 1988). Together, all of these analyses provide clues about the kinds of neural systems that may underlie attentional processes in humans and other mammals.

PLASTICITY

Both attention and memory provide significant plasticity in the nervous system, changing the pathways from receptors to effectors. Currently, the conceptual

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frameworks to describe the cognitive mechanisms involved in attention and memory are very different, and as compared to the substantial amount of information currently available about the neural mechanisms of memory, little information is available about the neural mechanisms of attention. What are the similarities and differences in these neural systems? The likelihood of them differing in fundamental neurobiological mechanisms, such as the flow of ions across membranes or synaptic currents, is very small, although possible. A more likely difference is in localization of function, the conjunction of neuroanatomical areas and neurochemical systems that respond to differences in attentional demands and mnemonic demands (Olton, Givens, Markowska, Shapiro, & Golski, 1992).

Considering the similarities and differences in the neural mechanisms of attention and memory can stimulate some useful thinking about attentional processes in a general cognitive/systematic/computational framework that is independent of the specific experimental procedures and limited theories that have been proposed so far. In both cases, the input/output functions of the nervous system have been changed by the addition of some other variable, attentional or mnemonic. How do these changes take place? What do the similarities and differences in neural mechanisms tell us about the distinction in the cognitive processes of memory and attention? Can this approach help to unify and integrate two fields that have developed relatively independently of each other, and most important, can it help to take the success that has characterized the neural analyses of memory and be equivalently successful in the neural analyses of attention?

In summary, the comparative analysis of attention in humans and other mammals provides opportunities to investigate the neural systems underlying attention. The seminal studies of Riley examining attention in animals provide an important building block for this enterprise, and if the goals of the research enterprise outlined here are achieved, Riley will have provided major links in the long chain of events leading to this success.

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Ode to Al

A retiring professor named Riley,
 Like the coyote, had an intellect wiley.
 With a voice deep and low,
 His wisdom he'd show
 With a humor expressed most dryly.

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